

Selection processes in arid Australia

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An important landmark in the recent development of evolutionary ecology was the publication of MacArthur and Wilson's (1967) *The Theory of Island Biogeography*. One of their innovations was the concept of *r*- and *K*-selection. In uncrowded environments *r*-selection favours high rates of population growth; it comes to the fore during colonizing episodes and in species that are frequently engaged in colonization. *K*-selection favours efficient use of resources and predominates in more crowded environments. The *r*-*K* concept has proved fruitful. Although it is not the only way of formulating questions, it provides a unifying framework with which to relate facts and ideas (Matthews 1976), and, given knowledge of an organism's habitat and bionomics, can be used to predict features of its population dynamics (Southwood 1977). The *r*-*K* concept also has its critics. They point out, for example, that it is not possible to classify all life history strategies on a single axis. This objection is answered if other axes can be recognized that have similar heuristic value. Wilbur *et al.* (1974) posed, as a challenge to evolutionary theory, the discovery of the number of dimensions necessary to account for the diversity of life histories shown by organisms. Natural habitats were described in terms of eight quantitative characters by Southwood (1977) who emphasized that time and space must be assessed against an organism's generation time and range of trivial movement. He condensed these characters into two axes, the *r*-*K* continuum and the adversity axis, or habitat predictability and habitat favourableness. These two axes define Southwood's habitat templet (Fig. 1) which is used here as the structure against which selection types are compared.

This account is aimed primarily at terrestrial arthropods but, with some modification, should be applicable to other invertebrates and vertebrates.

Three types of selection

K-selection operates in predictable favourable habitats, *r*-selection in unpredictable habitats, and a third selection type, for adaptation and conservation of adaptation, predominates in predictable but unfavourable habitats. It was first described as 'beyond-*K* selection', since it was recognized, during a study of a genus of tropical staphylinid beetles, in an altitude sequence in montane forests above a

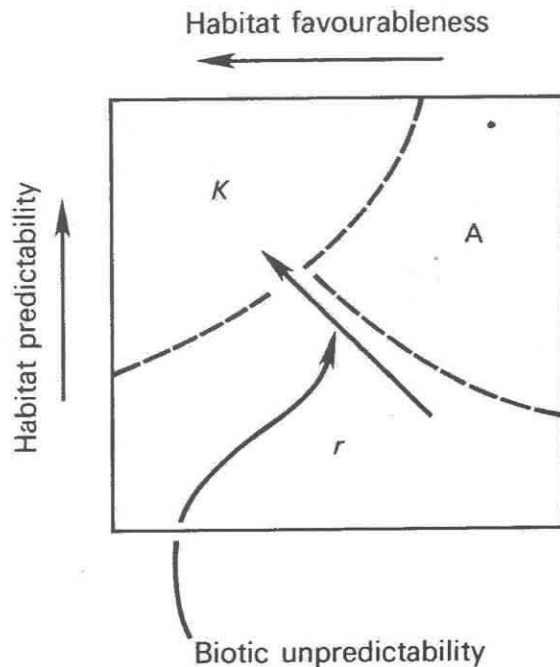


Fig. 1. The habitat templet, showing the distribution of three different types of selection. The lines separating the different types do not represent sharp boundaries but serve to indicate the areas in which each predominates. The actual form of the diagram is immaterial and depends on the scaling of the axes.

lowland forest zone of *K*-selection and a coastal zone of *r*-selection (P.J.M. Greenslade 1972 a,b). Whittaker (1975) briefly referred to three types of selection amongst which adversity selection is identical with beyond-*K* selection; his term is to be preferred and can be abbreviated as *A*-selection. His other two selection types, exploitation and interaction selection, can be equated with *r*- and *K*-selection respectively. All three of Whittaker's terms might well be used in order to avoid difficulties stemming from attempts to obtain precise definitions for *r*- and *K*-selection.

Table 1. Correlates of selection types

Correlate	Selection type		
	Exploitation, <i>r</i>	Interaction, <i>K</i>	Adversity, <i>A</i>
Habitat	Unpredictable	Predictable; favourable	Predictable; unfavourable
Community properties			
Species richness	Low	High	Low
Competition	Occasional; intense; simple, two species	Frequent or continuous; often complex, diffuse	Rare
Selection for:			
Migratory ability	++	+	-
Parthenogenesis	+	-	++
Dormancy	+	-	++
High potential reproductive rate	++	+	-
Resulting demographic features:			
Generation time	Short	Intermediate	Long
Population density	Variable, sometimes high	More constant, near carrying capacity	Low
Actual rates of increase	High	Intermediate	Low
Natality and mortality	Adult losses through mortality and migration	Juvenile mortality; variation in fecundity	Mortality at all stages; variation in fecundity and growth rates
Density dependence	Weak at low density; strong over-compensating at high density	Moderate, compensating	Weak

However usage of *r* and *K* is probably too well established to be abandoned and it does provide a convenient shorthand. Grime (1979) has developed a very similar idea of three types of selection. He described the determinants of vegetation as competition, disturbance and stress, each of which invokes a distinct set of ecological strategies. In this case habitats were classed by means of a triangular ordination and the *r*-*K* concept was not applied. However the two approaches are very similar and can be reconciled.

The correlates of exploitation, interaction and adversity selection are summarized in Table 1. For the first two selection types this is based on Pianka (1970), Southwood (1977) and Stubbs (1977). The correlates of adversity selection are derived from the staphylinid study (Greenslade 1972 a,b) and an account of adaptations of insects in the high arctic (Downes 1965).

Primary productivity, community complexity and species diversity all tend to increase with habitat favourableness and predictability (Southwood 1977) so that the habitat templet has a third element (Fig. 1), Glesener and Tilman's (1978) 'biotic unpredictability'. It can be expressed with a diversity index such as Hurlbert's (1971) 'uncertainty of encounter'. Interaction selection predominates in favourable habitats that can be relied upon to be suitable for reproduction over periods that are large in relation to an organism's generation time. In such habitats biotic unpredictability is high so that the crowding which defines this type of selection refers to crowding by other interacting species. Dobzhansky (1950) discussed the evolutionary significance of species interactions in favourable tropical environments, and Franklin (1978) has stressed the role of competitive interaction in evolution.

Further, it can be suggested that diffuse competition between one species and several others simultaneously (Terborgh 1971) is especially important under interaction selection and leads to reduction of niche overlap and specialization. Southwood *et al.* (1974) give a comprehensive account of interaction and exploitation selection although they do not clearly emphasize the significance of species interactions under the former.

Exploitation selection is associated with habitats that are only briefly favourable for reproduction during periods whose duration and recurrence cannot be predicted. Therefore it favours short generation time. In contrast, under adversity selection, periods suitable for growth and reproduction may be short and infrequent but life histories are often prolonged and development proceeds spasmodically whenever conditions are suitable. Consequently a feature of many adversity-selected populations is a heterogeneous age structure in which different generations and life history stages coexist. This coexistence has the selective advantage that particularly adverse conditions which might affect one stage more than another do not eliminate an entire population. Habitats in which adversity selection prevails are characterized by their predictable physical severity. If an organism can adapt to the severe non-biological environment, it has surmounted a barrier which protects it from harmful interaction with other organisms. It is no longer involved in the evolutionary race to cope with the pressures of a constantly changing biological environment. Conservation of adaptation also requires actual selection against genetic change and departure from the adapted type. This can be achieved by low rates of reproduction, long life-histories, reduced

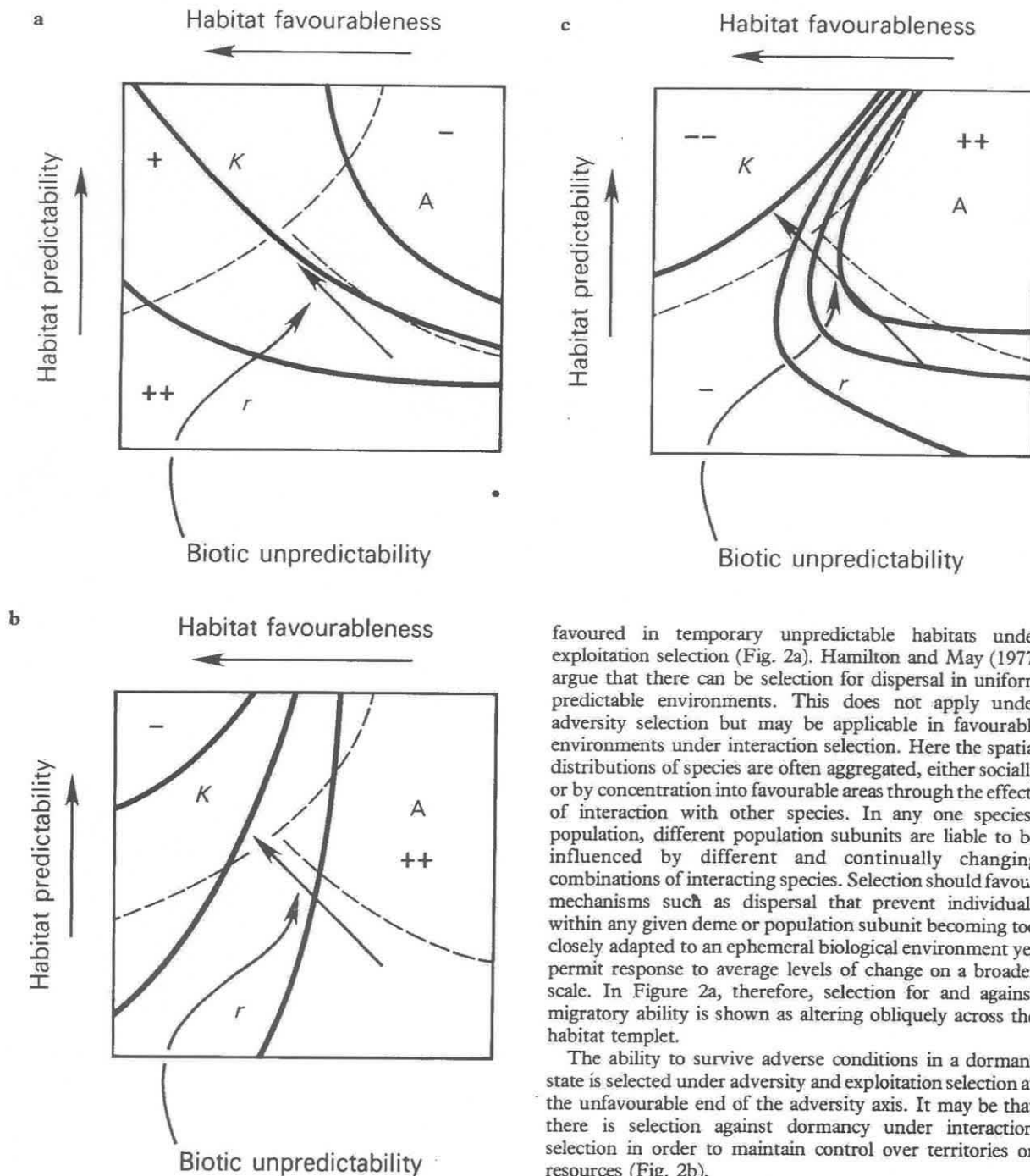


Figure 2. Selection for (+,++) and against (-,--) attributes: a, migratory ability, high reproductive rates; b, capacity for dormancy; c, parthenogenesis.

migratory ability (since dispersal can lead to loss of precisely adapted genotypes), and parthenogenesis.

Certain attributes of organisms are related to the habitat templet graphically in Figure 2. Migratory ability and high potential reproductive rates tend to be correlated and are

favoured in temporary unpredictable habitats under exploitation selection (Fig. 2a). Hamilton and May (1977) argue that there can be selection for dispersal in uniform predictable environments. This does not apply under adversity selection but may be applicable in favourable environments under interaction selection. Here the spatial distributions of species are often aggregated, either socially or by concentration into favourable areas through the effects of interaction with other species. In any one species-population, different population subunits are liable to be influenced by different and continually changing combinations of interacting species. Selection should favour mechanisms such as dispersal that prevent individuals within any given deme or population subunit becoming too closely adapted to an ephemeral biological environment yet permit response to average levels of change on a broader scale. In Figure 2a, therefore, selection for and against migratory ability is shown as altering obliquely across the habitat templet.

The ability to survive adverse conditions in a dormant state is selected under adversity and exploitation selection at the unfavourable end of the adversity axis. It may be that there is selection against dormancy under interaction selection in order to maintain control over territories or resources (Fig. 2b).

Glesener and Tilman (1978) related the occurrence of parthenogenesis to total environmental predictability, i.e. habitat predictability and biotic unpredictability. They found that normal, sexual reproduction was favoured by biotic unpredictability under interaction selection and in habitats low on the predictability axis. They also proposed that sexuality itself introduces unpredictability through the variability of the genotypes of interacting species. They summarized their conclusions in a diagram that is transferred to the habitat templet in Figure 2c. Parthenogenesis is permissible under adversity selection

where it has the advantage of reducing genetic variation, and, to a lesser extent, under interaction selection where it effectively doubles the potential rate of increase. Although it must be stressed that the areas of the habitat templet dominated by one type of selection or another do not have sharp boundaries (Fig. 1), an exception may be necessary for the interaction-adversity transition. Here interaction-selected sexuality should cause a sudden decline in the frequency of parthenogenesis as habitat favourableness increases.

Selection in arid Australia

When dealing with arid environments the two major axes of the habitat templet can be quantified most simply by using mean annual rainfall as a measure of habitat favourableness and its coefficient of variation as a measure of unpredictability. Alternatively, the mean annual period over which conditions are suitable for plant growth might form one axis and its predictability the other. A typical water-limited arid habitat with unpredictable rainfall can be placed at position 1 (F4, P4) on the habitat templet (Fig. 3).

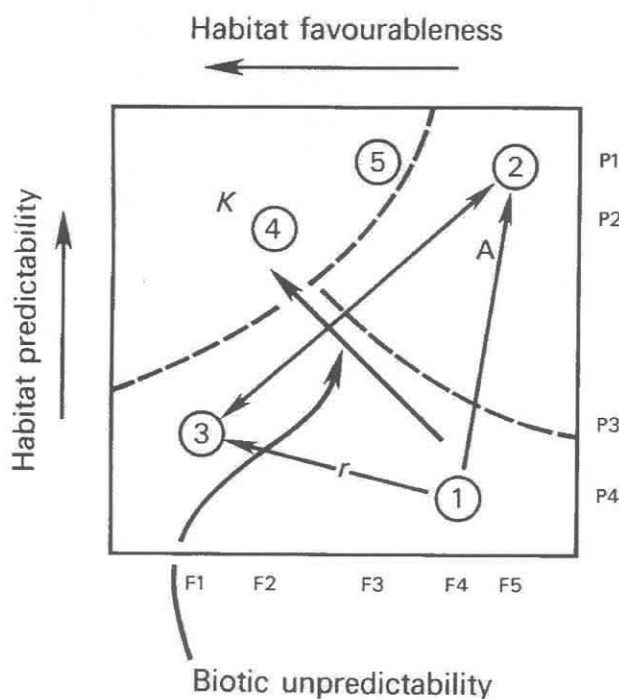


Fig. 3. Selection in the Australian arid zone (see text).

This probably describes the arid zone as perceived by large vertebrates with a relatively long life history, a large radius of trivial movement and few interacting species. But, for most organisms for most of the time, habitats in arid areas are predictable and severe, combining very high day-time temperatures at the soil surface, high evaporation rates and low productivity (position 2: F5, P1). Following effective rains they become, temporarily, much more favourable and even have something in common with the lowland tropics if neither moisture nor temperature is limiting. Extreme microclimatic regimes at the soil surface are moderated, there is a flush of plant growth and decomposer activity is

stimulated (position 3: F1, P3). Accordingly, two elements could be distinguished amongst the invertebrates of low shrubland in an arid locality in South Australia. One element was able to tolerate position 2 in Figure 3 and was more or less continuously active, even in hot dry weather. The other remained dormant until rain fell and was then active at position 3 (P. Greenslade 1975). Arid environments therefore provide opportunities for several different ecological strategies. The actual strategies that are available to a group are determined by basic morphology and physiology. In particular, the ability to survive in arid environments is strongly influenced by water and temperature relations, the capacity to enter desiccation-resistant, low energy-cost resting stages, and mode of locomotion. The last determines the scale over which migratory movement is possible and the ability to move into the soil, away from severe conditions at the surface.

In arid Australia some birds, Keast's (1959) 'interior nomads', appear to be the products of exploitation selection at position 3 (Fig. 3, Table 2). The distances over which they are able to migrate allow them to treat large areas of arid country as a system of scattered, temporarily favourable habitats. Cases of arid adaptation in Australian insects which Matthews (1976) regarded as a consequence of extreme interaction selection can be seen to be responses to adversity selection at position 2 (Fig. 3, Table 2). They include heterogeneous age structures as a result of partial hatching of egg populations at any one time, winglessness, low fecundity, a small or fractional annual number of generations, and prolonged flexible development periods. Some arid zone Collembola are parthenogenetic.

Table 2. Attributes selected according to position on habitat templet (see Fig. 3). This indicates the expected frequency of attributes in taxa or faunas. It applies primarily to invertebrates but may be applicable to higher vertebrates, for example if low metabolic rate can be equated with dormancy, and changes in the sex ratio with parthenogenesis.

Position on habitat templet	Selection type	Attributes under selection		
		Migratory ability, high reproductive rate	Parthenogenesis	Dormancy
1	r	+	-	++
2	A	-	++	++
3	r	++	-	+
4	K	+	---	-
5	K	+	---	+

An alternative strategy is to accommodate the demands of adversity or exploitation selection according to weather and/or subsequent changes in vegetation and population densities by switching between responses to positions 2 and 3 on the habitat templet (Fig. 3, Table 2). Migratory locusts that undergo phase changes are an example. The solitary phase persisting at low densities under unfavourable dry conditions appears to be adversity-selected while the migratory gregarious phase is exploitation-selected. Here movement between positions 2 and 3 occurs at the population level. In other groups individuals are able to switch from one set of adaptations to another and provide some striking contrasts in ability to become dormant.

At one end of the scale are the 'temporally dynamic reproductive strategies' of desert rodents which Nichols *et al.* (1976) discussed in terms of *r*- (or exploitation-), and *K*- (or interaction-) selection. In good years North American desert rodents are said to respond to exploitation-selection by showing a high prevalence of pregnancy, large litter sizes, early maturity and high population growth rates. In dry years reproduction is reduced and may be completely inhibited. The ability of populations to persist at low rates of reproduction and with few interactions with other species during unfavourable periods must be a response to adversity selection and not, as Nichols *et al.* suggest, to interaction selection.

Among Australian *Rattus* species the greatest potential reproductive rate is found in the plague rat, the arid inland form of *R. sordidus* (Breed 1978). Taylor and Horner (1973) referred to accounts of migrations by this rat at times of peak density. However, small rodents are ill-adapted to long distance migration, and irruption, a strong, overcompensatory density-dependent mortality process occurring at high population densities (Stubbs 1977), is typical of exploitation-selection. Such population movements do not appear to constitute migration in Johnson's (1969) sense of transference to new breeding habitats.

Rodents do not possess low energy-cost resting stages and must survive periods of adversity-selection in the active state. In their solitary adversity-selected phase, locusts have an intense egg diapause. The trend of increasing withdrawal from feeding, reproductive and locomotor activity in dry conditions culminates in invertebrates involved in the decomposition of organic matter. Some isotomid Collembola for example are polymorphic and switch between an active morph which can reach very high densities after rain (position 3, Fig. 3) and an inactive immobile desiccation-resistant morph at other times (Greenslade & Greenslade, in press).

The ants of arid Australia are exceptional in that many of them are the product of interaction-selection, experiencing arid environments as favourable and predictable (position 4: F2, P2 in Fig. 3). They are adapted to high temperatures, and can avoid excessively severe conditions at the soil surface in subterranean nests. They have indirect access to soil water in the form of exudates from deep-rooting woody plants, and the structure of shrubby, arid zone vegetation is optimal for their activities. The environment lacks other competing groups of similar diversity and the arid zone has accumulated many ant species. Community relationships are complex and are based on interaction-selected species associated with perennial vegetation (Greenslade & Greenslade, in press). Through their presence and activities these ants affect the selection process in other groups. Matthews (1976) describes the two dominant selection processes acting on the insects of mulga lands as drought and ants. In some cases ants increase biotic unpredictability and habitat favourableness if they become a resource for, or enter into symbiotic relationships with, other groups, thus imposing interaction selection. As abundant, general predators ants can also reduce habitat favourableness. Through their aggressiveness and ubiquity they add to environmental severity and many arid zone invertebrates must be 'ant-adapted' products of adversity selection. It would be consistent with this type of selection if further evolutionary development of such ant-adapted taxa was limited as the price to be paid for conservation of adaptation.

Discussion

In this account of selection types several important topics have only been referred to briefly or have not been mentioned; they will be dealt with in detail elsewhere. They include a full discussion of the correlates of adversity-selection, problems arising from MacArthur and Wilson's original definition and use of *r*- and *K*-selection, the position of α -selection for competitive ability, and the significance of diffuse interactions.

According to Figure 3, exploitation- and interaction-selection dominate habitats in arid Australia and neither is conducive to evolutionary diversification. Once adaptation to a severe physical environment is achieved, further evolutionary change is halted under adversity-selection. Where migratory ability is favoured by exploitation-selection any local adaptive genetic variation is likely to be lost through subsequent migratory movements. Migration can contribute to the evolution of new species and diversification if it leads to colonization of, and geographical isolation in, environments where interaction-selection prevails. Such environments lie in the semi-arid zone on the periphery of the arid centre, especially to the north, northwest (the Hamersley Ranges are semi-arid in some climatic classifications and have a markedly seasonal rainfall pattern), southwest and southeast. In these areas rainfall is somewhat higher than in the arid zone, but it is also strongly seasonal and much more predictable (position 5: F3, P1 on the habitat template in Fig. 3; Table 2). If dormancy, which can also stand for a variety of other morphological, physiological and behavioural adaptations to seasonal aridity, is retained or acquired, a new species may be pre-adapted to enter the arid zone itself. Consequently, according to Figure 3, the source of arid zone biota is likely to be the semi-arid zone. This even applies to ants. Among the meat ants, *Iridomyrmex purpureus* and allies, new species seem to arise in peripheral, semi-arid areas. In at least one case (small purple species: P.J.M. Greenslade & Halliday, this volume) this appears to have been followed by range extension into the arid zone. A hypothesis, yet to be tested, is that the high β diversity of local ant faunas in arid Australia results from the accumulation there of taxa whose main centres of radiation are, or have been, in northern and southern semi-arid areas.

Other examples of arid zone taxa with peripheral sources are cited by Maslin and Hopper (this volume). For the genus *Acacia* these authors suggest that many extant Australian species may, under one hypothesis, owe their origins to Quaternary climatic fluctuation. Hopper (1979) proposed that complex edaphic mosaics were in part responsible for rich endemic floras in semi-arid and sub-humid southwest Western Australia. The variety of soil landscapes to be found in arid and semi-arid Australia (Northcote & Wright, this volume) certainly contributes to high biotic diversity by permitting regional and local parapatric co-existence of taxa with diverse origins, amongst the meat ants for example (P.J.M. Greenslade & Halliday, this volume). However neither this factor nor climatic fluctuation can be regarded as a primary cause of rapid evolution. Instead it is suggested that the critical feature of the semi-arid zone is the operation of interaction selection, permitted by predictable seasonal climates. This suggestion is supported by the Quaternary history of northern hemisphere insect faunas. At one time it was believed that climatic fluctuation and associated contraction

and expansion of habitats would have led to extensive speciation and extinction (Coope 1978). In fact, northern insect faunas show little or no evolutionary change throughout the Pleistocene (Coope 1978, 1979). This can be

readily explained by the cold periglacial habitats that are involved and their position on the habitat templet, low on the favourableness axis and dominated by adversity and exploitation selection.

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